NOTES ON THE FLORAL BIOLOGY, CYTOLOGY, AND EMBRYOLOGY OF *CAMPYNEMANTHE* (LILIALES: CAMPYNEMATACEAE)[1]

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ABSTRACT

Field observations of the endemic New Caledonian genus *Campynemanthe* (Liliales: Campynemataceae) indicate that at least *C. neocaledonica* and *C. viridiflora* are strongly protandrous and have an unusual postanthesis recurving of the filaments. A chromosome number of $n = 11$ has been determined for both species from meiosis in pollen mother cells, these being first records for the genus and family. Endosperm formation in *C. neocaledonica* is nuclear rather than helobial as in several genera of the putatively related Melanthiaceae.

Campynemanthe Baillon comprises three species restricted to the Pacific island of New Caledonia. Goldblatt (1986) recently revised the genus along with the closely related, monotypic Tasmanian endemic *Campynema* Labill. and followed Dahlgren & Clifford (1982) and Dahlgren & Lu (1985) in placing both genera in Campynemataceae. The family, which appears to occupy an unspecialized position in Liliiflorae, is possibly most closely related to Melanthiaceae of the order Liliales (sensu Dahlgren & Clifford, 1982) or Melanthiales (as recently circumscribed by Dahlgren et al., 1985). Campynemataceae are distinguished from most other Liliales by their small greenish flowers with persistent and accrescent tepals, partly inferior ovaries, and free stylodia. The embryology of both genera of Campynemataceae is of the basic type for the monocots (Dutt, 1970; Dahlgren & Lu, 1985), except that the endosperm development is now known to be nuclear, a derived condition.

We report here some observations on the floral biology of two species of *Campynemanthe*, including the occurrence of protandry and an unusual postanthesis behavior of the persistent filaments. We also record the first chromosome counts for the genus and family, and we observed nuclear endosperm development, an aspect of the embryology of Campynemataceae previously unknown.

FLORAL BIOLOGY

Recent field observations indicate that *Campynemanthe neocaledonica* (Rendle) Goldblatt is strongly protandrous. This phenomenon was initially observed in December 1985, in a population of about 100 individuals covering an area of ca. 20 m^2 located at 900 m on the Plateau de Dogny (*Lowry 3945*). Many individuals were bearing both flowers and young fruits. The flowers exhibited discrete male and female phases of sexual expression. In the initial, male phase the straight filaments are erect to ascending and are usually twisted slightly counterclockwise so that the oblong to ovate anthers alternate with the tepals (Fig. 1a). During this phase the three small stylodia are erect and closely appressed, forming a short beak, with the undeveloped adaxial stigmatic surfaces unexposed. Following abscission of the anthers, the persistent filaments become nearly spreading to horizontal and twist further (Fig. 1b). At this time the stylodia elongate considerably and recurve to expose the whitish stigmatic surfaces.

While there appears to be no overlap in the sexual phases within a single flower, flowers of

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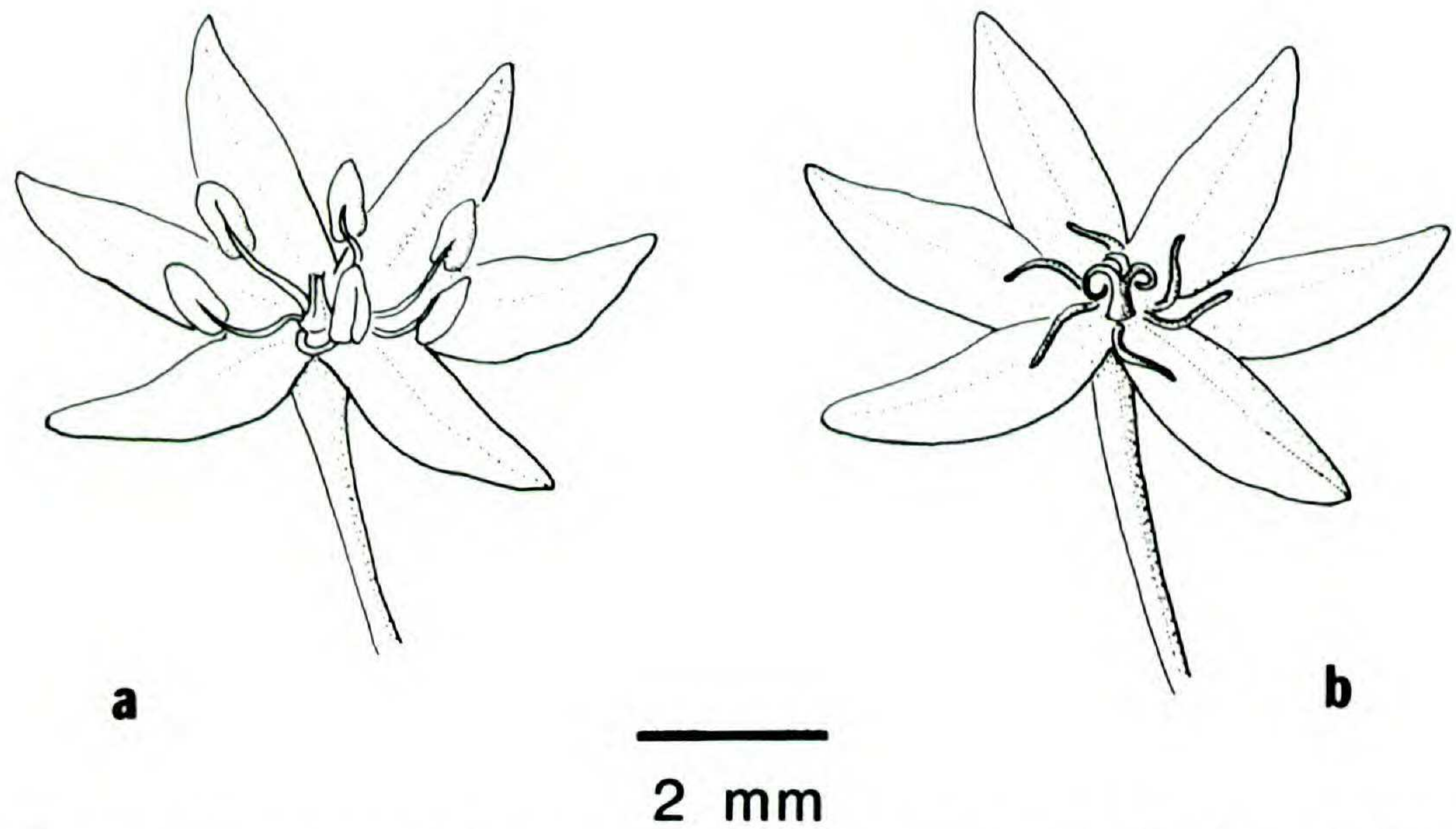

FIGURE 1. Flowers of *Campynemanthe neocaledonica* (*Lowry 3945*).—a. Male phase.—b. Female phase.

both phases frequently occur within individual inflorescences. Geitonogamy thus appears possible, assuming at least some self-compatibility. There did not appear to be synchrony of flowering among the individuals in the population, although observations were made on only a single day.

It has since been possible to confirm protandry in another population of *Campynemanthe neocaledonica* from Haute Ouinné (*Lowry & Suprin 3698*) from photographs taken in the field. Similarly, two distinct floral phases can be seen in photographs of *C. viridiflora* Baillon taken at 950 m on the Montagne des Sources (*Lowry 3762*) and at 1,350 m on Mt. Humboldt (*Lowry 3812*), indicating that this species is dichogamous and almost certainly protandrous. Unfortunately, we have not been able to determine whether protandry occurs in the third member of the genus, *C. parva* Goldblatt, or in *Campynema lineare* Labill. In the latter the filaments also recurve after abscission of the anthers, as figured by Dahlgren & Lu (1985) and reported by Goldblatt (1986).

Bawa & Beach (1981) and Lloyd & Webb (1986), who have reviewed the evolutionary aspects of dichogamy in general, and protandry in particular, concluded that dichogamy in self-compatible species permits pollen and stigmas to be positioned close to one another without high levels of self-pollination. They also pointed out that protandry is by far more common than protogyny in biotically pollinated species, which is presumably the case for *C. neocaledonica*. We did not observe floral visitors on species of *Campynemanthe*.

CHROMOSOME NUMBER

A haploid chromosome number of $n = 11$ was determined from pollen mother cells in flower buds of *Campynemanthe neocaledonica* and *C. viridiflora*. Inflorescences of these species were fixed in the field with 3 : 1 ethanol–acetic acid and squashed with FLP orcein. The relatively large chromosomes were ca. 3 μm long at meiotic metaphase but exhibited no distinctive details.

Chromosome numbers in Melanthiaceae are diverse. The counts summarized in Table 1 were taken from the *Index to Plant Chromosome Numbers* series (Goldblatt, 1985, et praec.) and unpublished work (Ambrose, 1975; Bodkin, 1978). Tofieldieae apparently have $x = 15$, the only known base number in the monotypic genera *Pleea* and *Harperocallis*, and the most common one in *Tofieldia*. *Tofieldia coccinea* Richards. has $x = 16$, a count confirmed by a number of workers, but several other species have $x = 15$. Counts of $n = 14$ and $n = 15$ have been reported for *T. calyculata* (L.) Wahlenb. *Japanolirion*, which perhaps belongs in Tofieldieae (Utech, 1984), has $n = 12$.

In Melanthieae $x = 8$ is the most frequent base number and the only one in *Melanthium*, *Schoenocaulon*, and *Veratrum*. There are two distinct series in *Zigadenus*: $n = 16$ in *Z. elegans* Pursh, *Z. glaucus* Nutt., *Z. sibiricus* (L.) A. Gray ex S. Wats., *Z. nuttallii* A. Gray ex S. Wats., and *Z. volcanicus* Benth.; and $n = 11$ in *Z. fontanus*

Eastw., *Z. fremontii* (Torr.) Torr. ex S. Wats., *Z. brevibracteatus* (M. E. Jones) Hall, and *Z. venenosus* S. Wats. *Amianthium* has $x = 16$ (Utech, 1986), and *Stenanthium* has $x = 8$ and a puzzling second base of $x = 10$.

Narthecieae, the largest tribe in the family, appears to be paleotetraploid. *Narthecium, Aletris, Nietreria*, and *Metanarthecium* have $x = 13$, while *Helonias* and *Heloniopsis*, now usually segregated as a distinct tribe (Utech, 1984) or even family, have $x = 17$. *Lophiola*, perhaps allied to Narthecieae, has $n = 21$.

The curious genus *Chionographis*, placed in Chionographideae (Dahlgren et al., 1985), has $n = 12$ in *C. koidzumiana* Ohwi and *C. japonica* (Willd.) Maxim. var. *japonica*, but *C. japonica* var. *kurohimensis* Ajima & Satomi has $n = 22$, and subspp. *minoensis* (Hara) Hara and *hisuachiana* (Okuyama) Hara have $n = 21$. The most parsimonious interpretation here is a base number of $x = 12$, with reduction to $x = 11$ and polyploidy resulting in $n = 22$, then reduction to $n = 21$. The taxonomically isolated *Xerophyllum* (Xerophylleae) has $x = 15$.

Summarizing, the available counts suggest to us a possible ancestral base number of $x = 8$ for Melanthiaceae, persisting only in *Melanthium, Schoenocaulon, Veratrum*, and *Stenanthium* (all Melanthieae). Other genera and tribes are apparently paleotetraploid, with Tofieldieae having $x = 15$ (or 16) and Narthecieae perhaps with $x = 13$. *Chionographis* most likely has $x = 12$, and *Xerophyllum* $x = 15$. The base number of $x = 17$ reported in *Helonias* and *Heloniopsis* is difficult to reconcile with other members of the Narthecieae. The odd counts of $n = 11$ in *Zigadenus*, which has several species with $x = 16$, and $n = 20$ in *Stenanthium*, which also has $n = 8$, remain to be explained as well.

Our report of $n = 11$ for Campynemataceae, which suggests a base number of $x = 11$, does not fit with any assemblage of Melanthiaceae. Campynemataceae do, however, appear to be paleotetraploid but have a lower base number than any genus or tribe of Melanthiaceae, with the exception of the paleodiploid *Veratrum*. This may indicate a derived condition, with $x = 11$ presumably being secondary to the higher numbers in the tetraploid series $x = 16, 14, 13, 12, 11$.

TABLE 1. Chromosome numbers recorded in Campynemataceae and basic chromosome numbers for genera of Melanthiaceae summarized from the *Index to Plant Chromosome Numbers* (Goldblatt, 1985, et praec.) and supplemented by data in Ambrose (1975), Bodkin (1978), and Utech (1984, 1986).

Taxon (species counted/total species)	Base Number	Haploid Numbers
Campynemataceae		
Campynema (0/1)	Uncounted	
Campynemanthe (2/3)		
C. neocaledonica[1]	11	11
C. viridiflora[1]	11	11
Melanthiaceae		
Tofieldieae		
Pleea (1/1)	15	15
Harperocallis (1/1)	15	15
Tofieldia (9/20)	15	15, 14, 16, 30
Japanolirion (1/1)	12	12
Melanthieae		
Veratrum (11/25)	8	8, 16, 40, 48
Zigadenus (8/15)	16	16, 11
Schoenocaulon (8/10)	8	8
Stenanthium (2/2)	8	8, 10
Melanthium	8	8
Amianthium	16	16
Narthecieae		
Narthecium (2/5)	13	13, 26
Aletris (7/25)	13	13, 26
Metanarthecium (1/2)	13	26
Nietreria	13	13
Ypsilandra (0/5)	Uncounted	
Helonias (1/1)	17	17
Heloniopsis (5/5)	17	17
Lophiola (1/1)	21 (or 7)	21
Chionographideae		
Chionographis (2/5)	12	12, 21, 22
Xerophylleae		
Xerophyllum (2/2)	15	15

[1] Voucher data for original counts: *C. neocaledonica*, New Caledonia, Plateau de Dogny, 900 m, *Lowry 3945* (MO, NOU, P); *C. viridiflora*, New Caledonia, Mt. Mou, 1,150 m, *Lowry 3857* (MO, NOU, P).

EMBRYOLOGY

Although it was not possible to pursue the details of early endosperm development in *Campynemanthe*, the available fixed material of *C. neocaledonica* (*Lowry 3945*), which comprised nearly 100 seeds that had developed past the 64-nucleate stage, indicates that the endosperm of this species is nucleate and not helobial (Stenar,

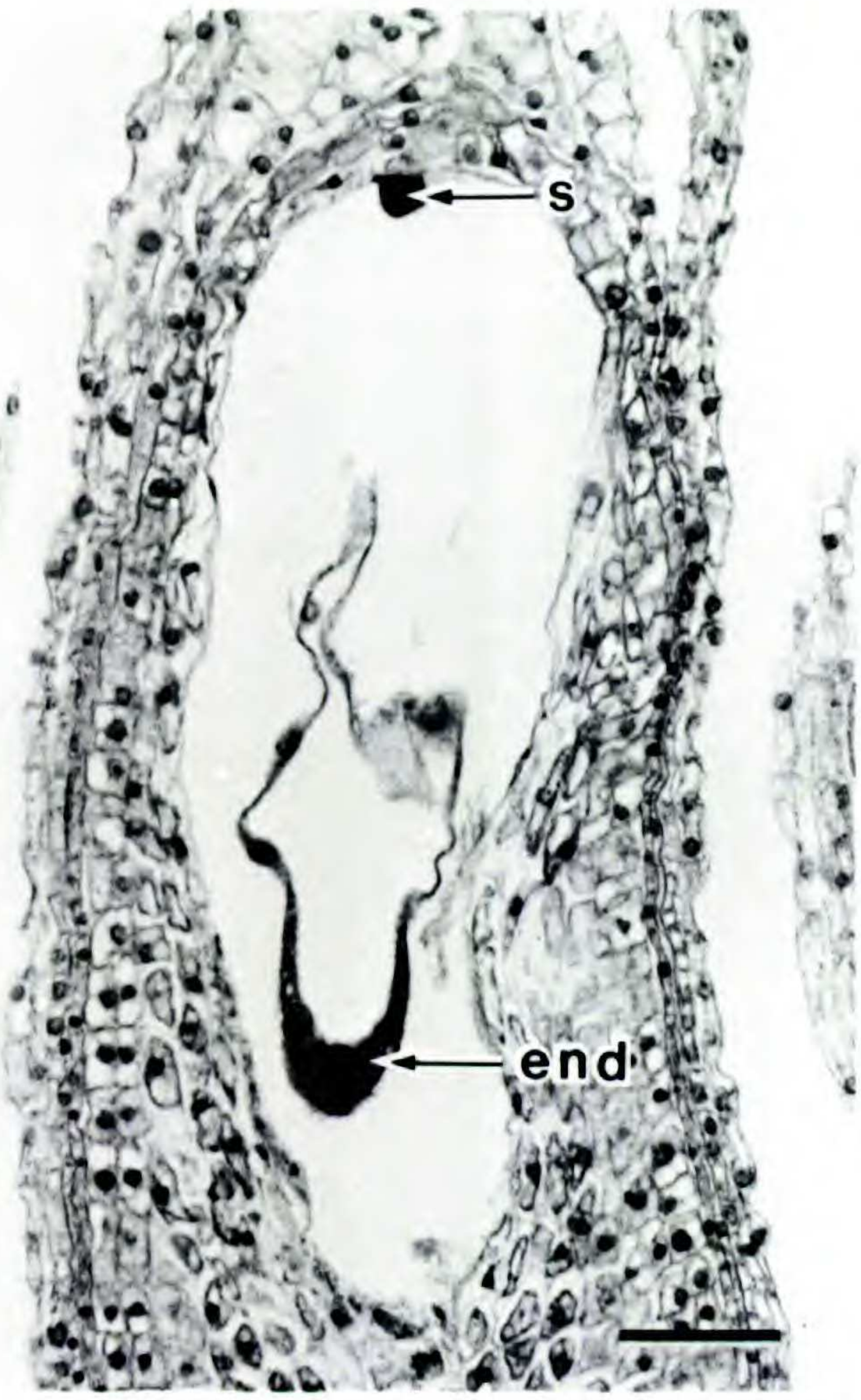

FIGURE 2. Longitudinal section of a young seed of *Campynemanthe neocaledonica* showing free endosperm nuclei at the 64-nucleate stage. s, synergid; end, endosperm nucleus. Scale = 50 μm.

1949; Eunus, 1951) as in other Melanthiaceae in which this embryological feature is known (including *Tofieldia, Narthecium, Heloniopsis, Metanarthecium, Aletris, Zigadenus, Veratrum,* and *Amianthium*). In *Amianthium muscaetoxicum* Walt. the embryo sac in postfertilization stages forms a micropylar and chalazal endosperm chamber characteristic of the helobial type; in an earlier stage the micropylar chamber contains 16 nuclei, and the chalazal chamber 8 nuclei (Eunus, 1951, fig. 31). In *Campynemanthe,* however, there appears to be no such chalazal chamber, nor is there a distinct aggregate of endosperm nuclei at the chalazal end. All of the endosperm nuclei occur within a single cell (i.e., embryo sac), although they are more abundant toward the chalazal end (Fig. 2). The presence of nuclear endosperm in *C. neocaledonica* suggests that this character may be useful in distinguishing Campynemataceae from Melanthiaceae.

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